THE MODE OF LIFE OF *ARENICOLA MARINA* L.

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(Text-figs. 1–10)

CONTENTS

INTRODUCTION

Large, common, tough, the lugworm is an outstandingly good object for anatomical and physiological work. Its mode of life has not yet been clearly worked out, and one must know how an animal lives if one wishes to understand its structural and functional peculiarities. Burrowing as it does in muddy sand, the lugworm cannot be watched under natural conditions (except on the rare occasions when it shows itself on the surface). Existing accounts of its behaviour in the field are therefore practically confined to the form of the burrow which it excavates. The present paper attempts to synthesize, partly from field observations and partly from laboratory studies of the worm's activities, a coherent picture of its daily life.

The work was done in the summer and autumn of 1944, while the Zoology Department of University College, London, was evacuated to Bangor, North Wales. My warmest thanks are due to Professor Brambell and his staff, of the Zoology Department, University College of North Wales, for their friendly and helpful reception during that period.

The present content of the literature on the lugworm's burrow may be summarized in three statements: (i) according to the great majority of writers, the worm lives in a U-shaped burrow, open at both ends; (ii) a minority believe, however, that the open U is atypical, and that the usual burrow form is an L, in which a U-configuration is completed by a column of sand, distinguishable from the general mass, and rising from the lower end of the L to the surface; it is to this opinion that the present writer adheres; (iii) other burrow forms have been described from time to time, but appear in fact to be untrue, or true only in exceptional cases. The following are the main points in the history of the subject.

The first definite mention of the lugworm was by Belon (1555), who stated that it lives in mud, into which it can burrow rapidly, that it is dug for bait, and that its presence is indicated by masses of coiled excrements on the surface. For nearly three hundred years, practically nothing was added to this account of its mode of life. Detailed descriptions of the form of the burrow began to appear in the nineteenth century.

The U-shaped burrow was introduced by Audouin & Milne Edwards (1833) in the following words: the worms 'creusent des cavités cylindriques très profondes, qui communiquent ordinairement au dehors par deux extrémités'. Note the qualifying word 'ordinairement'. Milne Edwards repeated this description, with the qualification, in his revision of Lamarck (1838).

Stannius (1840) collected *Arenicola marina* at Heligoland, for anatomical study. He failed to find two openings to the burrow, and stated that the experience of fishermen, whom he questioned on the point, agreed with his own.

In spite of the dissentient voice of Stannius, the worm was described by the great majority of subsequent writers as living in a U-shaped burrow. Usually the statement was made without qualification, as if the open U were the only observable form. Fauvel (1927), to quote a recent example, described the burrow of *A. marina* as a 'galerie en U' without alternative.

An obvious question arises. If the lugworm lives in a U-shaped burrow, open at both ends, whence does it get the sand which it so copiously defaecates?

According to many of the earlier writers (e.g. Stannius, 1840; Gamble & Ashworth, 1898), burrowing and feeding are one and the same act; the lugworm burrows by eating its way into the sand. The view has, however, gradually grown up that the two performances are in fact distinct, and it was recently shown that very little sand, if any, is swallowed during burrowing (Wells, 1944 *b*). Those who believe that the open U is the typical burrow form generally state that the worm ascends to feed from the surface layer of the sand, which is especially rich in micro-organisms and detritus.

The first hint of this came from Cunningham & Ramage (1888): 'sand is ejected in a cylindrical rod from the anus, and this forms a spiral coil on the surface of the shore; near the "cast" is usually a wide hole, from which the head is protruded when the tide is up.'

Gamble & Ashworth (1898) made an almost identical statement. They distinguished, on anatomical grounds, between two varieties of *A. marina*. The large 'Laminarian' variety was described as living in a long vertical shaft (p. 175). The worms of the commoner 'littoral' variety 'sink their U-shaped burrows to a depth of from one to two feet below the surface. One end of the burrow is marked by a casting, the other by a "countersunk" hole, through which the head of the lugworm is protruded when the tide comes in.'

Wesenberg-Lund (1905) was more specific. He described the burrow as horseshoe-shaped, with a faecal pile at one end and a funnel-shaped depression at the other. At low tide, the worm lies at the bottom of the burrow. When the tide comes in, carrying and depositing fresh material, the worm ascends and sucks surface sand from the region of the funnel. This is how the funnel is formed.

Blegvad (1914) watched the worms on the beach, when the sand was covered by a shallow layer of water. 'At the bottom of a little funnel-shaped depression of the sand the proboscis may be seen moving up and down, swallowing the matter drawn down from the sides and circumference of the funnel.'

In the light of these various observations, the open U is seen as a workable burrow form, in which the worm could live and maintain itself. The writer believes, however, that the U is exceptional, occurring only in a particular type of situation, and he doubts whether the worm ever actually feeds at the surface, even when its head moves about in the funnel. As we shall see, it may be doing something else.

The first clear account of the L is by Bohn (1903), who worked at Wimereux. He believed that many varieties of *A. marina* exist, with different habits, but he gave details of two only. One of these was described as making a reticulate burrow (p. 175). The other was found on a bank of sand exposed at low tide. When the sea was just leaving the bank, and the surface sand was soft and semi-fluid, he saw the formation and disappearance of fugitive funnels. The level of the water in the funnels oscillated rhythmically, and sometimes dropped abruptly, as if sucked down from below. The worms' heads did not appear at the surface. As the sand dried and hardened, the funnels became fixed. Only in exceptional cases was there an opening at the bottom of the funnel. The burrows were nearly always oblique or L-shaped, with their blind ends dilated (Fig. 1 b_1, b_2). The head of the worm was at the blind end, 10–15 cm. below the surface, and vertically below the funnel. As the head moved rhythmically and swallowed sand, the column of sand above it was kept in pulsing and slowly subsiding motion, and the funnel at the surface resulted from this activity.

Ashworth (1912) mentioned L-shaped burrows as an occasional alternative to the open U.

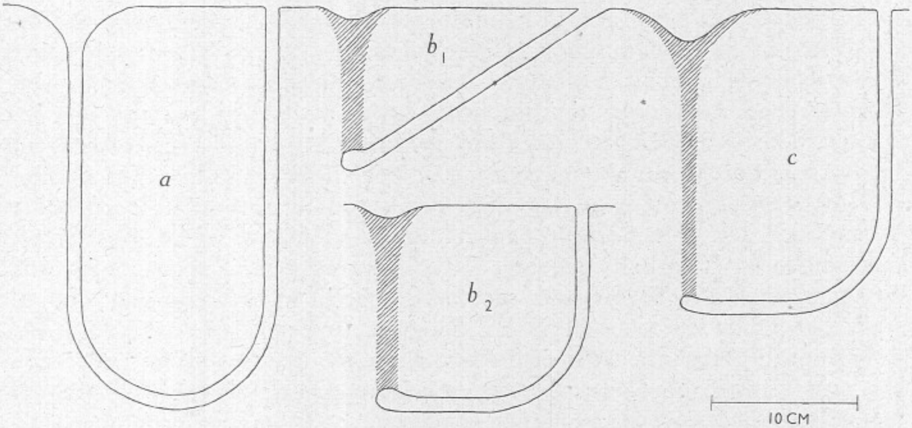

Fig. 1. Diagrams of *Arenicola* burrows from the literature. *a* is the open U. b_1, b_2 are of Bohn's low-tide variety; the shaded area is a column of rhythmically moving sand over the animal's head. *c* is Thamdrup's typical form; the shaded area is the 'Saugsäule', continually consumed below and renewed by sedimentation and subsidence from above.

The fullest description of the L is that of Thamdrup (1935), who worked on beaches in Denmark, in Holland, at Plymouth and at Millport, and wrote that he had examined many hundreds of lugworm burrows, all of which conformed to the same essential plan. His account is in many ways the best yet available; nevertheless certain of his results will be disputed below, and it is therefore necessary to summarize his conclusions in some detail.

Thamdrup's main points are as follows. Starting from the faecal pile, a gallery descends vertically, or in a gentle curve, to a depth of 20–28 cm., where it turns to run horizontally for a variable distance. It thus forms an L. This L does not necessarily lie in a plane, but may bend to one side or the other. In exceptional cases, the blind end of the gallery may rise 1–5 cm. towards the surface. The worm is generally found with its head in the lower part of the burrow, and its tail towards the opening. Vertically above the blind end of the burrow, there is in most cases a conical depression on the surface of the sand. This is connected with the end of the burrow by a narrow, perpendicular column of yellow sand, the 'Saugsäule', contrasting in colour with the grey-black of the general mass (Fig. 1 *c*). The column arises as follows. The worm eats sand at the blind end of the gallery. New sand slides downwards to replace the old, as fast as it is consumed. The surface therefore subsides to form a funnel, in which fresh material is deposited by the tide. Thus a continually descending column of surface sand originates and is maintained. Sometimes the worm tunnels a horizontal branch from the lower part of the burrow, and sets up a new 'Saugsäule' at the end of it.

Thamdrup adds a tantalizing sentence: 'Diese ganze Auffassung von der Bildung der Röhre und dem Entstehen des Trichters und der Saugsäule durch die Nahrungsaufnahme wurde beim Auslegen rotgefärbten Sandes auf die Oberfläche kontrolliert; hierdurch war es möglich, die Bewegung des Materials durch den Trichter und die Saugsäule hindurch Schritt für Schritt zu verfolgen, bis es als Kothaufen wieder an die Oberfläche gelangt.' No further details are given on this point—nothing except the passage just quoted. This is unfortunate; the concept of the 'Saugsäule' will be criticized below, and more information about the reddened sand might be illuminating.

Why, if the burrow is of this form, have so many authorities described it as an open U? Thamdrup's explanation is as follows. The gravity-feed mechanism only works if the sand is sufficiently moist to slide downwards. In some situations, at low tide, the water content of the sand may become such that, while the material in the 'Saugsäule' continues to descend as fast as consumed below, the sides of the funnel are too dry to slide in and renew the supply from above. In this case, a large part, or even the whole, of the material in the 'Saugsäule' may be removed by the worm. The 'Saugsäule' may thus be converted into an open shaft, completing the U, 'als ob der Wurm seinen Gang unter der Bildung eines U an die Oberfläche geführt hatte. In solchen Fällen kann man auch ab und zu sehen, wie der Wurm sich in dem so gebildeten Gang hinaufstreckt.'

Thamdrup's whole story is clear and attractive, and rests on a great number of field observations. Nevertheless, there are facts which it fails to explain. Why, for instance, when an accident of desiccation has converted the L into an open U, should the worm stretch up towards the funnel? As we have seen, the worm's head has been described as appearing actually at the funnel by Cunningham & Ramage (1888), by Gamble & Ashworth (1898), by Wesenberg-Lund (1905) and by Blegvad (1914); this impressive series of observations suggests that it is something more than a chance phenomenon. One may also ask how a worm, living in such a burrow as Thamdrup describes, obtains an oxygen supply.

It will be shown below that the lugworm's burrow is typically an L with a column of 'specialized' sand completing a U-configuration, but the column is the resultant of a number of different factors; its form is more variable than Thamdrup's account suggests, and it is set up and maintained by several distinct activities of the worm.

Besides the open U and the L, a few other burrow forms have been described; they appear, however, to occur in exceptional cases only, if they occur at all.

Oken (1817) stated that the lugworm lives, head upwards, in a vertical shaft, about as long as the worm itself. Nothing like this has been observed by anybody else.

Gamble and Ashworth (1898) distinguished between two varieties of *A. marina*, differing in structure, in habitat and in habit. The common 'littoral' variety was described as living in an open U. The second 'Laminarian' variety 'occurs on the Lancashire coast at the upper part of the Laminarian zone...the burrows are of considerable length, three feet or more, and are not U-shaped, but simply vertical'. As Fauvel (1899) suggested, a worm living in such a shaft would have to get food and oxygen by means quite unlike those employed in a U or an L, and so great a difference of habit is hard to conceive. The description of Gamble & Ashworth was later revised by Ashworth (1912), who placed the worms of the 'Laminarian' variety either in vertical shafts or in L-shaped burrows, the latter being the more usual form. The writer believes that all of the vertical shafts were in fact L's whose horizontal parts had eluded the observers. In digging in the Laminarian zone, to a depth of 'three feet or more', the holes would readily fill with water, and this, as he can testify, makes careful study difficult. Richter (1926) included the vertical shaft among the possible burrow forms of *A. marina*, but he apparently based this statement on the work of Gamble & Ashworth, and not on his own observation.

Irregular networks of galleries, branching out from the bottom of the burrow, were briefly described by Bohn (1903) as occurring in aquaria, and by Richter (1924) as occurring in the field.

The Form of the Burrow, as Observed in the Neighbourhood of Bangor, North Wales

My field observations were made from July to October 1944, at several localities in the neighbourhood of Bangor, North Wales.

The technique varied with the circumstances. If the sand was firm enough, it was caused to split in the plane of the burrow. If this was impossible, the sand was sliced with a trowel or a large knife, or the burrow was followed with a long probe of bicycle valve tubing.

Owing to the great variability of the burrow, the following account is illustrated as far as possible by scale drawings of individual burrows. The drawings were carefully made on graph paper on the beach, after measuring up the burrows with a ruler, and subsequently traced on to Bristol board. To facilitate comparison, the drawings have been turned round when necessary, to bring the faecal end always to the right.

The burrows generally curve somewhat to right or left, and are drawn as if straightened out to lie in the plane of the paper.

In every case where an individual burrow was drawn, the worm was found and roughly measured. The outlines of the worms have been included to scale in the drawings, though, for clarity, they have not been put in place in the burrows.

The Three Divisions of the Burrow

In the great majority of burrows, a tunnel descends vertically from just below the pile of faeces on the surface and then swings round to run horizontally. So far everything is plain; most authorities agree up to this point, and the roughly L-shaped tunnel is very easily demonstrated on the beach. The worm is found in the tunnel, with its tail towards the faecal opening, and, on careful inspection, certain distinguishing marks can be seen, which differentiate the upper few centimetres of the tunnel from the rest. The short, upper portion will be termed the *tail shaft*, and the longer portion, which descends from the lower end of the tail shaft and then curves to become horizontal, will be termed the *gallery* (Fig. 10, p. 204).

It is at the lower end of the gallery that the difficulties, and most of the interest, begin. This end of the gallery is connected with the surface by a zone which will be termed the *head shaft*. The characters of the head shaft are exceedingly variable, from burrow to burrow and, probably, in a single burrow from time to time. Sometimes a clear channel continues upwards from the end of the gallery to the surface of the sand, in which case the burrow is an open U. More often, the U-configuration is completed by a column of specialized, or 'worked' sand, rising from the deep end of the gallery, and broadening, more or less regularly, and more or less rapidly, as the surface is approached. Shafts of this type are often difficult to expose and study.

The simpler, less variable parts of the burrow will be described first.

The Gallery

The gallery—the longest of the three divisions of the burrow—is a cylindrical passage along which the worm moves to and fro, always with its head in the same direction.[1] The inner surface of the wall is firm and well smoothed, except that it generally shows a fine transverse striation, presumably due to the worm's neuropodia.

If the burrow runs through grey or black mud, the gallery is seen to be surrounded by a yellow-brown layer, often several millimetres thick. This layer is generally firmer than the surrounding mud, due, apparently, to mucus exuded by the worm. Its colour is largely caused by the oxidation of black iron sulphide in the mud to yellow oxide, but sometimes it exhibits greenish or rusty orange tints, to which coloured secretions from the worm probably contribute.

The gallery usually drops more or less vertically for some distance from the lower end of the tail shaft, and then curves gradually round to become horizontal. Occasionally, however, one finds a burrow which descends obliquely, at about 45°, from the defaecation point.

[1] By narrowing itself, and repeatedly extruding its proboscis along its own ventral surface, a lugworm can turn longitudinally in a glass tube which, at other times, it seems comfortably to fill. This may also occur in sand. I have noted on several occasions that worms kept in the laboratory can turn in their burrows, thereafter defaecating from the upper end of the head shaft. Once or twice, in the field, I saw faecal cylinders in the middle of funnels, suggesting that the worms had reversed themselves in their burrows. Reversal appears, however, to be an infrequent event, involving reconstruction of the burrow to suit the new orientation.

The Tail Shaft

Periodically, the worm moves backwards to the surface to defaecate. This it does by shooting out, at great speed, a single faecal cylinder. The caudal end of the burrow therefore becomes surrounded by a number of cylinders, each resulting from one such excursion. If there is little wave disturbance, the cylinders may pile up into a heap several centimetres in height.

Defaecation usually occurs with the tip of the tail just at the surface of the sand—at least, the faecal cylinders usually end at the very mouth of the burrow. Occasionally, however, one finds a cylinder extending for a few millimetres down a burrow.

The tail shaft is that part of the burrow which is occupied by the tail at the moment of defaecation. It is generally strictly vertical (except for the uppermost few millimetres). It differs from the gallery in being slightly narrower, and, since it is never occupied by the chaetigerous part of the worm, in showing no transverse, neuropodial striations.

The uppermost extremity of the tail shaft may open simply and directly at the surface of the sand. More often, it bends sharply, so that the upright part of the shaft is not vertically below the orifice (Fig. 5 *b*). Very commonly, it divides into two or more branches which open separately, and through any one of which the worm may defaecate (Fig. 3). Clearly, these passages must have been excavated and moulded by the tail itself.

The Head Shaft

As already stated, the head shaft is extremely variable. I have chosen for description the commonest and most representative types, and also one or two out of many exceptional or unique cases; the latter were selected, partly to show the range of variation encountered, and partly because they throw light on the activities of the worms.

The examples chosen will be grouped according to the kind of bottom in which they were found.

In rapidly drying sand. At Aber, when the tide is out, a flat expanse of sand stretches seawards for several miles. The surface undulates gently, and varies in moisture relations from place to place. Vast areas keep a certain amount of water on the surface, even after hours of exposure, and these are densely populated by large lugworms. Here and there, however, a stretch is found which dries soon after the tide has receded. The worms on such patches are few and, perhaps because they are young, or perhaps because the environment is unfavourable, they are never of large size. The surface of these patches is firm and ripple-marked. As one digs, no water appears in the holes, and it is often obvious, at least after an hour or so of tidal exposure, that the worms in the burrows are living in damp air.

The burrows in such places are very easy to study. If one inserts the spade vertically beside a funnel, on the side away from the casting, and then gives a quick heave, the sand often splits in such a way as to expose the whole burrow in section. Other types of bottom are less amenable. Rapidly drying sand will therefore be taken first, even though the small size and sparse distribution of the worms suggest that the habitat is not as favourable for the inhabitants as it is for the observer.

The positions of the head shafts are generally indicated, on the surface of the dry sand, by shallow conical depressions. Sometimes there is a hole, a few millimetres across, at the bottom of the cone; sometimes there is no trace of any opening. The hole, when present, suggests that the burrow is an open U, but this inference is dangerous; as we shall see, the hole may lead into a blind cavity; the only way to establish the presence of an open U is to expose it along its whole length. Occasionally, a head shaft ends above in a ragged hole, a centimetre or so across, and lying flush with the surface, i.e. without any surrounding depression.

The commonest type of burrow is that illustrated by the two examples in Fig. 2 *a*, *b*. In both there is a shallow cone ending below in a small opening; this opening leads into an irregularly shaped cavity whose walls are apparently smoothed. From the bottom of this cavity, a tubular passage descends to continue into the lower end of the gallery. In Fig. 2 *a*, this passage is empty, and the burrow is therefore an open U. There is, however, a difference between the gallery and the passage ascending the head shaft. The wall of the gallery is firm and transversely marked by the worm's neuropodia. As the burrow curves upwards into the head shaft, these signs disappear, and the ascending passage has coarse, powdery looking walls. In Fig. 2 *b*, the general plan is similar, but the upper end of the passage is filled with a cylinder of fairly firm sand (stippled in the drawing) which can quite easily be tumbled out of it.

Such burrows were found in great numbers. The sand cylinder may be short, or it may descend as far as the boundary between head shaft and gallery; sometimes it continues above into a mass of sand filling the lower part of the irregular cavity below the funnel. The passage up the head shaft has the same diameter as the gallery, from whose lower end it curves smoothly upwards; it differs from the gallery only in the coarse texture of its wall; it has evidently been excavated and traversed by the worm. The sand cylinder seems to have been drawn down into it.

The most reasonable explanation of these appearances is, I think, the following. At high tide, when the surface sand was soft, the worm ascended and worked, by some means, on the sand in the region of the irregular cavity below the funnel, mixing it with water and making it semi-fluid. The worm then retired backwards to the gallery, drawing the softened sand down as a cylinder. This gives Fig. 2 *b*. To get Fig. 2 *a*, one must suppose that the cylinder was consumed from below.

As already stated, Fig. 2 *a*, *b* show the most usual type of burrow found in dry sand. Sometimes, however, one finds a head shaft consisting of a broad cone of yellowish, 'worked' sand. Two examples of this are drawn in Fig. 2 *c*, *d*.

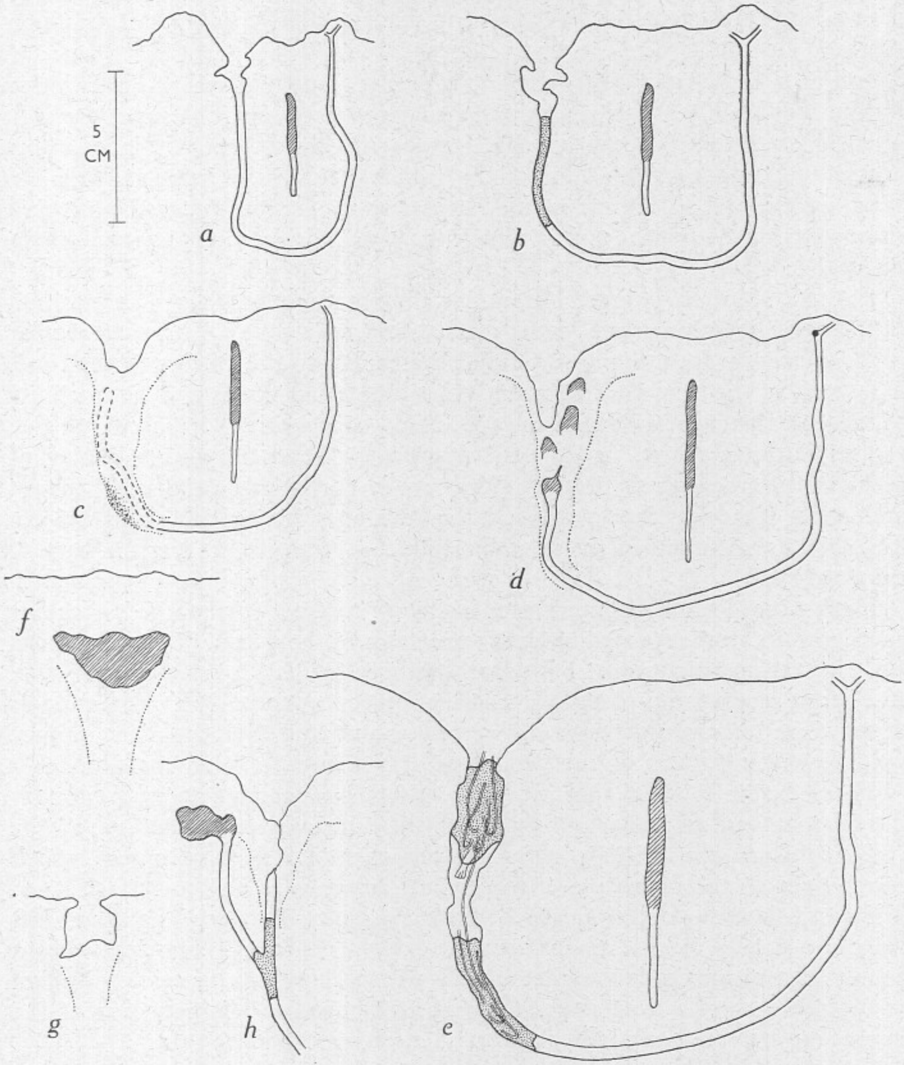

Fig. 2. Burrows and head shafts from rapidly drying sand, Aber. *a–e*, whole burrows, with the worms inset to scale; *f–h*, head shafts. The scale applies to all the figures.

In Fig. 2 *c*, the head shaft is a broad column of yellow sand (dotted outline), fine in texture except at its lower end, where it is coarse and gritty (stippled). The lumen of the burrow continues up this column to end blindly near the base of the surface depression, but, as before, the part which ascends the column (dashed outline) has coarse, powdery walls and is less permanent in appearance than the gallery. The sand in the column was probably worked up and softened by the worm at high tide; the ascending tunnel represents a single upward excursion of the worm, made while the sand was still fairly soft.

In Fig. 2 *d*, the head shaft is again a tapering column of yellow sand (dotted outline). Within it, four cavities (shaded) appeared when the sand was split open. The cavities have fairly smooth walls; the lowest one continues into a descending passage, which meets the gallery below; this passage lacks the usual gallery markings. The cavities appear to result from successive upward excursions of the worm, during which the sand was eaten or dragged downwards.

Fig. 2 *e* shows a unique, but rather illuminating, burrow. The position of the head shaft is marked on the surface by a wide cone. A broad, irregular space curves up from the lower end of the gallery to the bottom of the cone. The walls of this space are apparently smoothed, but not as firm and definite as those of the gallery. Within the space, and completely blocking it, are two masses of rather moist, 'pasty' sand (stippled). There are also a number of filaments of green weed (double lines), mostly curled up in the sand masses, and, at the bottom of the upper mass, the skeleton of the tail of a small shrimp. The worm was found in the usual position, i.e. with its head at the base of the head shaft.

Fig. 2 *e* can, I think, be interpreted in one way only. The smoothed, irregular cavity results from repeated upward excursions of the worm. The moist sand, with its various inclusions, has somehow been pulled down into the shaft. As the tide recedes, bits of algae and similar objects are often left in the funnels of lugworm burrows; if the worm were to ascend and drag the moist surface sand downwards, such objects would be drawn into the head shaft too.

These examples show that previous writers have tended to over-simplify the burrow, and the behaviour by which the burrow is produced.

To conclude this section, some further examples may be noted, which throw light on the formation of the conical depressions on the surface.

Fig. 2 *f* shows a condition which I only encountered once. The head shaft ends above in a closed, smooth-walled cavity (shaded). This cavity lies a couple of centimetres below the surface, which shows no depression or sign of the presence of a head shaft. This shaft belonged to a large worm, as the worms on dry sandbanks go; its overall length was about 9·5 cm.

Fig. 2 *g* shows a not uncommon condition. The head shaft leads up to an irregular cavity whose roof has apparently collapsed in the middle. This condition can clearly be derived from that just described, if it be supposed that the worm had worked rather nearer the surface. The appearance, as seen from above, of a ragged hole without a surrounding depression indicates a shaft of this type; by inserting a probe, one can generally satisfy oneself that the hole leads into a fairly extensive, blind cavity.

Finally, Fig. 2 *h* illustrates an exceptional condition, which I saw only twice out of many burrows examined—a forked head shaft. The vertical branch ends just below the funnel, to which a fine crack runs from its blind end. The side branch ends beside the funnel, in a cavity with rather smoothed walls (shaded). This may have been the beginning of a second funnel. Sand (stippled) has been dragged down to the fork, apparently from the original funnel. The worm's overall length was about 4 cm.

In wet sand (*the* '*typical form*'). As already described, the distribution of lugworms on the Aber sands is somewhat patchy. The areas densely populated with large worms have the following characteristics: the sand surface is fairly firm and ripple-marked; the receding tide generally leaves water in the troughs of the ripples and the hollows marking the positions of *Arenicola* head shafts. This water may remain for hours, or it may slowly dry or drain away, but even in the latter case the deeper sand is obviously wetter than on the 'rapidly drying' patches described above. Water collects in the holes as one digs, making observation difficult.

The burrows in wet sand conform to a fairly simple and uniform pattern. For this reason, and because the worms are large and abundant, the wet-sand form will be termed the 'typical' one.

I studied the typical form at Aber and at Bangor, on the beach below the lane called Gorad-y-Gyt. In the latter situation, much of the sand contains shell fragments, which lead to complications described in another section. If, however, one walks out along a stream which crosses the sands to the right (north-east) of a disused oyster bed, one finds, near low-tide mark, a patch where the shell is practically absent and the burrows conform to the simple, typical pattern.

The presence of a head shaft in wet sand is usually marked by a saucer-shaped depression of the surface, several centimetres across. In most cases, these depressions retain water as the tide recedes, and fragments of weed and similar objects collect in them. Sometimes a hole, about 1 cm. across, opens at the bottom of the saucer. This is no proof that the burrow is an open U; in every case examined by myself, the hole led into an irregular, blind cavity, as in Fig. 3.

On exploring the saucers with the finger, one notices (i) that the bottom of the saucer, which is usually flat, is softer than the general sand, and (ii) that, at a certain point, the finger can be pushed downwards into a tapering shaft, encountering practically no resistance; the shaft is often long enough to admit the whole forefinger, and several centimetres wide at the top; it feels as if full of a fluid or semi-fluid mixture of sand and water.

Owing to the wet consistency of the sand, one can seldom expose the head shafts by causing it to split. One has to slice away the sand with a trowel or a large knife, and study the shafts in horizontal or vertical section. The burrow drawn in Fig. 3 was fortunately placed in a bank of sand beside a stream, and could therefore be dissected from the side and drawn to scale.

The upper part of the head shaft consists of a more or less gradually tapering cone of pasty or fluid sand. This is the part that one can probe with the finger, as just described. It leads below into an approximately vertical column of rather firmer sand, which descends to meet the gallery. This column has the following characteristics. It is yellow in colour, contrasting with the grey or black of the surrounding sand; its boundary is sharp, but completely

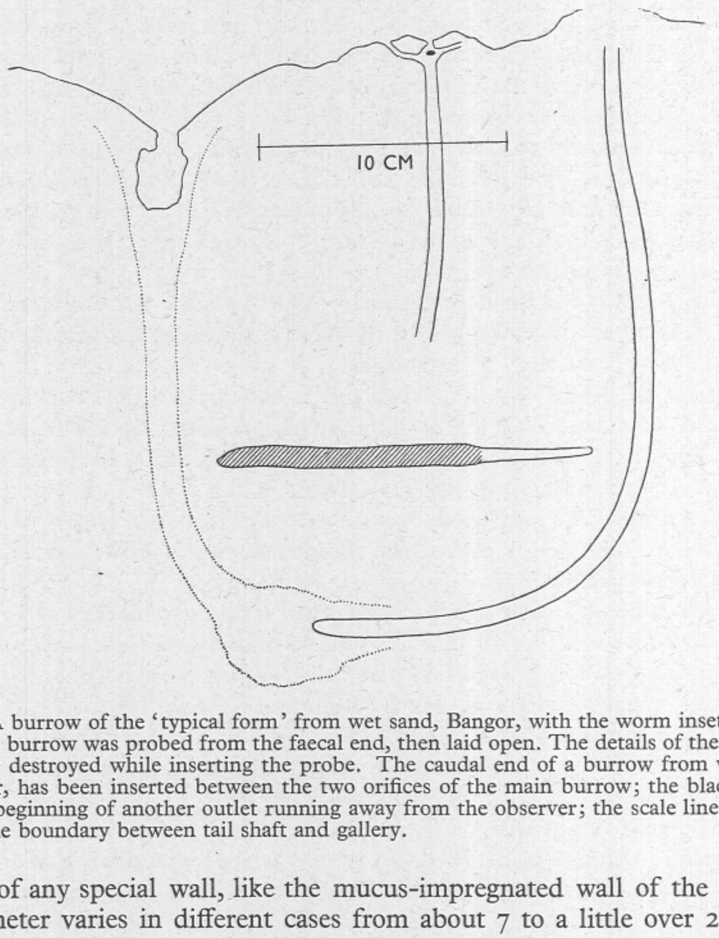

Fig. 3. A burrow of the 'typical form' from wet sand, Bangor, with the worm inset to scale. This burrow was probed from the faecal end, then laid open. The details of the tail shaft were destroyed while inserting the probe. The caudal end of a burrow from wet sand, Aber, has been inserted between the two orifices of the main burrow; the black spot is the beginning of another outlet running away from the observer; the scale line is drawn at the boundary between tail shaft and gallery.

devoid of any special wall, like the mucus-impregnated wall of the gallery; its diameter varies in different cases from about 7 to a little over 20 mm.; it enlarges, and becomes irregular in form, at the point where it meets the gallery.

The yellow column is obviously the 'Saugsäule' of Thamdrup (1935). His suggestion that its component sand is continually consumed below, and therefore continually moving downwards, is supported by the following observations. Bits of weed and similar objects (including dead leaves, on the Bangor beach in autumn) often collect in the saucers on the surface.

Sometimes one finds a piece of weed or a leaf, still quite fresh in appearance, embedded in the sand at some point along the shaft. Finally, in the enlarged region where the shaft meets the gallery, there is often a considerable accumulation of weed, shell, leaves and so forth, mostly packed against the sides of the yellow area. They seem to be drawn in above and to travel down with the sand, to be rejected by the feeding worm, and so to collect at the point where feeding takes place.

On the other hand, there are facts which make it impossible to accept Thamdrup's hypothesis as the whole truth. Sometimes one finds a shaft dropping perpendicularly to the end of the gallery, as his hypothesis requires (Fig. 1 *c*). Very often, however, the shafts are curved. Sometimes the end of the gallery begins to rise, and the head shaft smoothly continues the curve. Once or twice, I saw a gentle sigmoid curvature of the shaft.[1] These curves make it impossible that the shafts could have originated, and improbable that they could be maintained, by gravitational subsidence alone. Subsidence is undoubtedly important, but other factors must be at work in giving the shaft its form.

Three facts suggest that the worm tunnels up nearly to the surface as a first stage in the setting up of the head shafts. First, the narrowest head shafts observed were just about equal in diameter to the galleries. Secondly, they often curve upwards, in such a way as smoothly to continue the line of the gallery. Thirdly, I once found the following appearances: a cone of soft sand, 10 cm. deep and 6 cm. across at its upper end, tapered below into a shaft, slightly over 1 cm. across; in the upper end of the shaft, there was a long cylindrical cavity, of the diameter of a fair-sized worm's body, ending above in a slight dilation at the bottom of the cone, and continuing for some distance down the shaft; unhappily, my excavation filled with water as I was working and I could neither determine whether the cavity traversed the whole shaft nor find the responsible worm, but it seems clear that the worm had ascended the shaft to the cone, while the latter was full of sand.

These evidences suggest that the narrower head shafts originate in much the same way as that of Fig. 2 *b*. The worm ascends nearly to the surface, 'works up' and softens a cone of sand, and then retires, drawing the softened sand into the shaft after it. Such a sand column could then operate for some time as suggested by Thamdrup, sliding down as consumed below. The wider head shafts, which range up to about 2 cm. across, might originate as narrow ones, and then be widened, either by parallel workings of this type or by other factors to be discussed in a later section.

[1] Once I followed a column, about 1 cm. in diameter, which ran as follows: starting from the lower end of a cone of very wet sand, 4 cm. deep, it (i) descended for 6 cm. through black muddy sand, then (ii) passed downwards for a further 10 cm. through a layer of sand closely packed with small shell fragments, during which part of its course it curved gently round the edge of a larger shell and returned to the original perpendicular, and finally (iii) swung, pretty sharply, through a right angle, to meet the gallery, where the head of a large worm (overall length 16 cm., and plump in proportion) was found.

The presence of a saucer on the surface indicates a well-established head shaft. Sometimes one sees other appearances which (as shown by laboratory observations, described below) are preliminary stages in the development of saucers. The following are examples: (i) one or two cracks, running circularly and marking out an area a couple of centimetres across, which is flush with and otherwise indistinguishable from the general surface; (ii) a roughly circular area of surface sand, a couple of centimetres across, which has dropped about 1 cm. and so forms the flat bottom of a pit surrounded by vertical walls; (iii) an irregular hole, 1–2 cm. in diameter, leading into a blind cavity much as in Fig. 2 *g*.

Such incipient shafts are always to be seen here and there among the saucers. Once, at Bangor, after several days of stormy weather, I found that the saucers were few and small while most of the head shafts were marked by appearances like those just described. Deeper in the sand, I found the usual yellow columns; probably the storm had disturbed the surface sand only, and it was the uppermost portion of each shaft which was being re-developed.

In shelly sand. At Bangor, below Gorad-y-Gyt, most of the sand contains numerous shell fragments, which lead to curious complications. I studied the shelly burrows mainly on a patch to the left (south-west) of the old oyster bed, near the inshore margin of the sand flat.

The sand here is very wet, muddy and soft. The worms are large and abundant. The surface signs of a head shaft are like those described for wet sand; the most usual one is a shallow, water-filled saucer, with pieces of weed and so forth left in it by the receding tide.

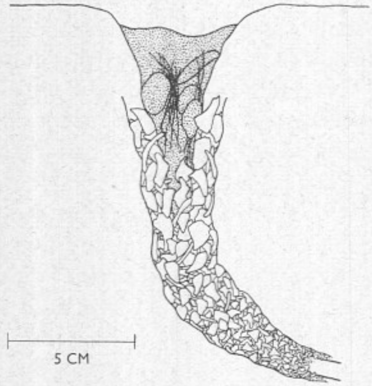

Fig. 4. Generalized drawing of the head shafts in wet, shelly sand, Bangor.

If one follows a burrow, starting from the faecal end, one finds that it descends and turns horizontally in the usual way. One then encounters a roughly cylindrical mass of closely packed shell fragments, which curves upwards and rises towards the surface (Fig. 4). The shell fragments are finer at the base of the mass, and become coarser as one ascends; among them one finds occasional bits of weed. The most curious thing about the mass is that the fragments are 'washed', and have very little sand or silt between them, so that the mass as a whole is loose in texture and crumbles very readily. Sometimes the lumen of the burrow can be traced for some little distance into the shelly mass, sometimes not; it is here, at the base of the mass, that the worm is usually found.

In most cases, a cone of soft, fluid sand can be seen to descend from the saucer at the surface into the shelly mass. As in the case of the wet-sand shafts, this cone can be probed from above with the finger. It often contains shells, or pieces of shells, or weed; these are still unwashed, or muddy, and appear to be descending with the sand from the surface. A cluster of such objects is shown in Fig. 4.

Once or twice, I was able to find a narrow cylinder of fairly firm sand, descending through the shelly mass from the point of the cone. In such a case, the head shaft can be described as one of the typical wet-sand form, surrounded by a shelly sheath. If the worm works the shaft by tunnelling upwards and then dragging softened sand down, one can see that coarse shell fragments might be pushed aside by the ascending worm and so form a sheath. Rejection of the finer fragments could occur during feeding from the bottom of the shaft. More often than not, however, I failed to find the sand cylinder; there seemed to be nothing but a wet cone above, a gallery below, and, in between, the crumbling, baffling mass of miscellaneous fragments.

The fact that the fragments are washed is probably due to the action of the current of water with which the worm irrigates its burrow, to get a supply of oxygen. This current, as will be shown in a later section, ascends the head shaft, and could carry the lighter particles away.

Because of the fluidity of the sand cone, and the friability of the shelly mass, the head shafts cannot be neatly exposed and dissected. Fig. 4 is a generalized drawing, made after digging out and examining a great number of shafts.

A raised bank crosses the patch where most of these observations were made, running roughly parallel with the shore. The sand on the bank is very shelly, and as firm as rapidly drying sand, which it also resembles in the paucity and small size of its worms. I was able, by splitting the sand on the edge of this bank, to expose in section the two burrows drawn in Fig. 5 *a*, *b*. Their general form is not unlike that of the dry-sand burrows in Fig. 2 *c*, *d*, but they are greatly complicated by the presence of shell fragments.

In Fig. 5 *a*, the lumen of the burrow vanishes into a conical region, composed below of sand and fine shell bits, and above of rather larger, silt-free fragments. Resting on top of the shell is a mass of moist, yellow sand (fine stippling in the figure). On dissecting with a knife, I failed to find any upward extension of the lumen, or downward extension of the sand, into the shelly mass. It was, however, very difficult to examine.

In Fig. 5 *b*, the lumen is traceable (to the left of the thick ascending line in the figure), first past a collection of fine, neatly packed shell fragments (dashed), then through a mass of coarser, washed shell. At the upper end of this passage (which is walled, most of the way up, simply by clean, loosely packed shell pieces) there lies, across its top, a large shell (drawn as a thick, oblique line). Curving to the left of this shell, the passage ends at the foot of a cone of yellow sand (fine stippling). The sand may have extended for some distance down the passage as a cylinder; unhappily, the other half of the split sand broke up and could not be examined. This shaft might have arisen by the means postulated above. The coarse shell could have been thrust aside while the worm was working up and down in the shaft, then washed by the ascending water current. The collection of fine fragments below could have resulted from rejection during feeding.

In any case, it is clear enough that the burrows fail to conform with any of the simple patterns to be found in the literature, and must have been set up by complicated activities of the worms. The fact that the worms are large and numerous on the wetter parts of the area shows that the observations

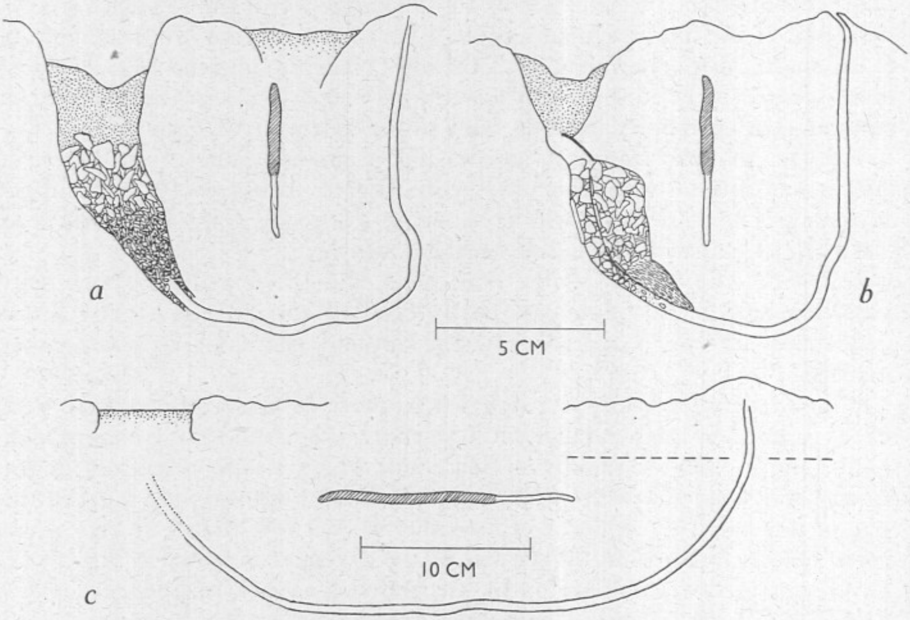

Fig. 5. *a*, *b*, burrows from firm, shelly sand, Bangor; *c*, burrow from gravelly sand, among stones, Pwllfanog.

cannot be dismissed as trivial. In places the head shafts, active and abandoned, are so plentiful that their horizontal portions (which are often longer than in Fig. 4) form an irregular layer of almost slit-free shell, about 15 cm. from the surface—a very definite contribution by the lugworm population to the architecture of the beach.

In gravelly and stony situations. We conclude with an atypical habitat, which is interesting as showing what a lugworm can do.

Near a disused slate factory at Pwllfanog, on the Anglesey side of the Menai Straits, a mass of rock and large pieces of slate stretches out into the tidal zone. The whole is overgrown with *Fucus*. Here and there, among the rocks and slate slabs, small patches with a sandy surface appear, and on these one occasionally sees the casts of quite large *A. marina*. The burrows can be traced downwards, using a long, flexible probe, into a layer of gravelly sand with numerous stones and small pieces of slate.

I found the burrows, and especially the head shafts, impossible to expose completely. One has continually to remove stones, and, as one does so, the structure of the loose, gravelly material breaks up. My most successful attempt is shown in Fig. 5 *c*. The details of the faecal end were destroyed by the insertion of the probe. From this point, the burrow dropped vertically through about 4 cm. of coarse sand, then (at the dashed line) entered a gravelly layer, in which it swung round to become horizontal. The gravelly layer consisted mainly of fine stones, 2–3 mm. across, but there were many smaller grains and larger objects, including stones 5 cm. or so across.

The horizontal part of the burrow ran over the surface of a firm, compact stratum. It was crescent- or banana-shaped, as viewed from above, and has been 'straightened out' in the drawing. It ended by curving upwards, and here a large worm was found.

The worm's head was vertically below a flat area of sand, several centimetres across and surrounded by largish stones; this area was the upper end of the head shaft. The sand below it was about 3 cm. deep, and lay on a layer of loosely packed gravel in which the gallery ended; surface sand and bits of *Fucus* appeared to have been pulled downwards between the stones by the worm.

Though very imperfect, this description shows that the animal could not possibly have set up a 'Saugsäule' in the manner described by Thamdrup. It must have maintained itself by working its way up through the gravel and either eating the surface sand *in situ* or dragging material down for consumption below.

Once, at Pwllfanog, I found a large *A. marina* in a thin layer of silty material between two large, flat, horizontal slabs of slate. Unfortunately, the form of its burrow could not be determined.

Conclusions from the field observations. The main conclusions, drawn from the above examples, will now be summarized.

(i) The open U is an atypical burrow form. It was encountered in rapidly drying sand only, a situation where the worms were few and small. Very often, in other situations, small round holes were seen at the bottoms of funnels; a casual observer might take this appearance as evidence of a U-shaped burrow; in most cases, however, the hole leads into a blind cavity, and the only way to establish the existence of an open U is to expose it along its whole length.

Moreover, the two limbs of the U, when it occurs, have distinct characteristics. The ascending passage in the head shaft differs markedly from the gallery in the loose, 'powdery' appearance of its walls, and in the absence of neuropodial markings. It seems to be of less permanent nature than the gallery.

(ii) The most typical form of head shaft is an ascending column of yellow sand, spreading out into a cone below a saucer-shaped depression of the surface (Fig. 3). That the shafts are fed from at their lower ends, and consequently subside gradually, is shown by the accumulations of pieces of weed and similar objects which are often found at their bottoms, and by the surface saucers, which are evidently due to subsidence. Nevertheless, the head shaft cannot originate or be shaped, as Thamdrup suggested, by these means alone. The shafts are sometimes curved, even in wet, shell-free sand, and the worms can live and maintain themselves in shelly and gravelly situations where the setting up of a shaft by deep feeding and subsidence would be quite impossible. The narrowest head shafts seen in wet sand, and the upward passages in the open U's, correspond in diameter with the gallery, and there is no reason, on Thamdrup's hypothesis, why this should be so.

(iii) There is abundant evidence that the worms actually ascend the head shafts from time to time. Passages obviously left by the worms were often seen in rapidly drying sand, and once in wet sand. In the latter situation, the head shafts seem, from their diameters, to be formed in the first place by upward excursions of the worms. The appearance of a shelly sheath surrounding a cylinder of sand, sometimes seen on the shelly beach, suggests that the shell was thrust aside during the upward excursions. The conclusion seems inescapable, that the worm ascends the head shaft to 'work up' and manipulate the sand. Such head shafts as those in Figs. 2 *a*, *b* and *e*; 5 *a*, *b* and *c* could only have arisen in consequence of complicated 'working' operations.

The Working of the Head Shaft

In explaining the appearances seen in the field, the worm was supposed to 'work up' and soften the sand in the head shaft, and, in some cases, actively to draw it downwards. We turn now to a laboratory study of the means by which the worm could do these things.

The Irrigation of the Burrow, and the Effects of Water Currents on the Sand

As many observers have remarked, a lugworm resting in a glass tube drives water through the tube by means of special waves travelling along its body, usually from tail to head (Just, 1924; van Dam, 1937, 1938). This is so invariable a component of the worm's behaviour in the laboratory that its normality—i.e. its occurrence at high tide in the field—can hardly be doubted. The current is generally regarded as a means of irrigating the burrow, and so securing a supply of oxygen.

This is all very well if the burrow is an open U. Often, however, the open part of the burrow is L-shaped, and the U is completed by a column of sand. Problems therefore arise. Can a closed burrow be irrigated at all? If so, what happens to the stream at the blind end of the L, where the worm's head usually lies? Sea water being lighter than sand, the current will presumably make its way upwards, and may therefore have an important effect on the architecture of the head shaft.

To explore this possibility, I made a number of experiments of the following kind. Glass vessels were filled with muddy sand from an *Arenicola* beach at Bangor, and currents of sea water were then discharged into the sand near the glass, so that their subsequent course and their effects on the sand could be watched.

Measurements of the amount of water pumped by lugworms were made by van Dam (1938). He put the worms in glass tubes. In most of his experiments, the worms were driving water from one vessel to another, and the levels in the two vessels were equalized by a system of siphons, i.e. the worms were not pumping against a measurable pressure head. He found, under these conditions, (i) that the worms pumped intermittently; thus, in a protocol which he cites in detail, a worm pumped for about 10 min., then rested for about 20 min., and so on; (ii) that the waves could be reversed, so that the current could be driven in either direction along the body, but it 'practically always goes from tail to head'; (iii) while a worm was pumping, about 8 waves travelled along its body per min., and each wave drove slightly over 1 c.c. of water down the tube. He also made the following remark: 'I observed that *Arenicola* is able to force water through its tube against a pressure of 10 cm. water.' This is not given as a maximum value, but simply as an incidental observation. The maximum pressure obtainable was not determined, and no measurements were made of the volumes pumped when working against pressure heads.

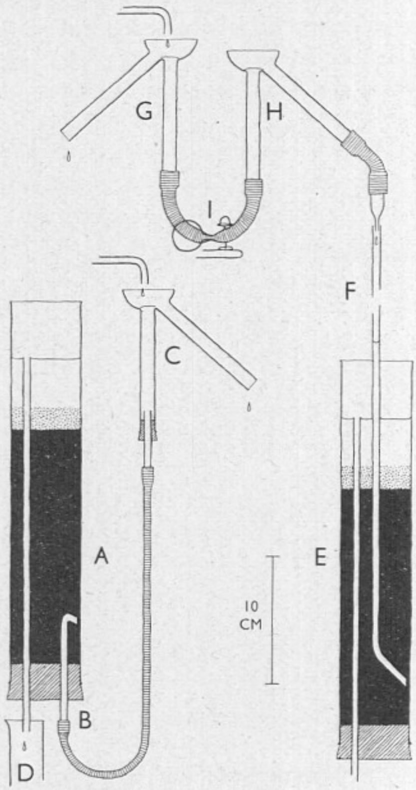

Fig. 6. Apparatus for studying the effects of artificial irrigation currents on the sand. Explanation in the text.

Experiments with controlled pressure. My first experiments were made at constant pressures, using the apparatus shown on the left in Fig. 6. In a typical experiment, the apparatus is filled with sea water, and muddy sand from the beach is added to glass cylinder *A* (internal diameter 5·5 cm.) and gently stirred, then allowed to settle for an hour or so. There results a column of muddy sand, pretty firmly packed (black in Fig. 6), with a layer of light material, which sediments slowly, above it (stippled). Sea water is then allowed to flow in through inflow tube *B* (internal diameter 0·7 cm.), which opens about 2 mm. from the side of the cylinder, so that the course of the stream can be observed. The percolation pressure is regulated by adjusting the height of overflow vessel *C*, and the rate of percolation is measured by means of graduated cylinder *D*.

The results were curious; the flow was almost 'all or none'. For instance, an experiment in which the inflow hole was 10 cm. below the top of the mud gave the following results. The 'percolation pressure' is the difference between the water levels in *A* and *C*. With percolation pressures up to 5·5 cm.,

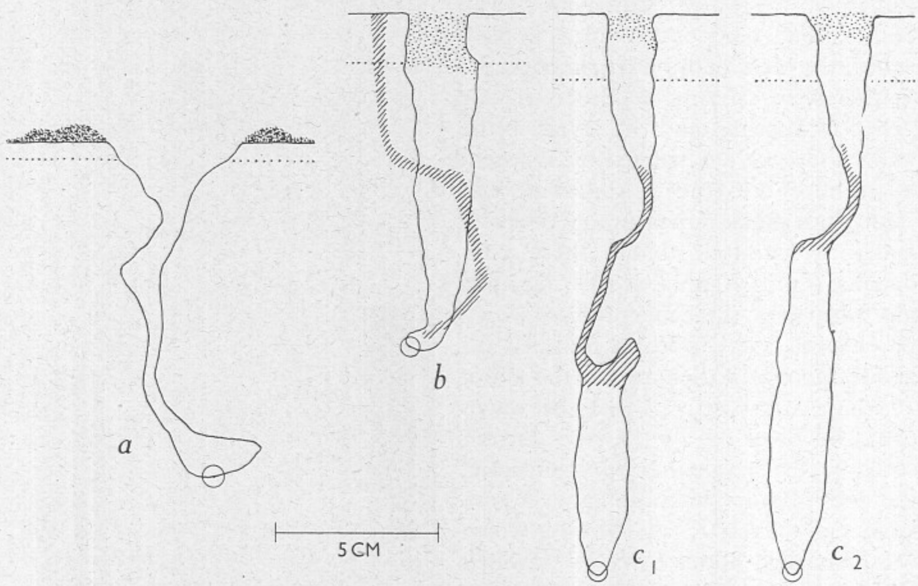

Fig. 7. Channels made with the apparatus of Fig. 6. Explanation in the text.

no displacement of the sand occurred, and there was no flow. With 6·0 or 6·5 cm., fine cracks appeared, running irregularly upwards, through which the water filtered very slowly, at about 0·2 c.c./min. At the threshold pressure (7·0 cm.), the water blasted itself an upward channel, through which it rushed at 250 c.c./min. The channel is drawn to scale in Fig. 7 *a*, as seen through the glass. The circle indicates the inflow hole, about 2 mm. back from the glass. The cylinder was filled with muddy sand up to the dotted line, and a layer of light sediment, resting on this, up to the continuous line. The channel ends above in a 'volcano'. The 'crater' is surrounded by a rim of upblown sand (stippled). The lower part of the channel has been blown entirely clear of sand; the 'crater' cone contains a violent swirl of the heavier sand grains (not drawn)—falling, then being blown upwards again, and so on—and the lighter, muddy components have been completely swept away.

With greater depths of sand, similar 'all or none' flow was obtained. The pressure required to blast a channel was usually about equal to the depth of the sand; thus, with 20 cm. sand over the inflow hole, a percolation pressure of 19 cm. gave a slow trickle of 0·5 c.c./min., while 21 cm. pressure blasted a channel and produced a violent flow.

Experiments with controlled flow rate. A flow of 250 c.c./min. is beyond the capacity of any *Arenicola.* I therefore made a second series of experiments, in which the flow rate was controlled instead of the pressure. The current was made to flow in pulses, in imitation of the irrigation waves, so that it should resemble the output of a lugworm as closely as possible.

The apparatus is shown in Fig. 6, on the right. Glass cylinder *E* is filled with muddy sand as before. Sea water is admitted through vertical tube *F* (internal diameter 0·6 cm.). Tube *F* receives the water from the 'pulsing flow' device. Overflow vessel *G* is connected to a similar vessel *H*, set slightly below it, by wide rubber tubing closed by pinchcock *I*. The lower flange of the pinchcock is soldered to a brass rod, rigidly held in a stand. Its upper flange bears a hoop of copper wire, through which a length of leather belting (not drawn) is passed. The ends of the belt pass downwards and are tied below a crank on an axle of a Palmer power table. With every revolution of the crank, the belt is pulled down and so opens the pinchcock, allowing *G* to discharge into *H*, and so over into *F*.

The crank revolved once every 7 sec. The heights of *G* and *H* were set to give 1 c.c. at each discharge. These quantities were based on the results of van Dam (1938) on living lugworms, cited above.

Several experiments were made, with sand columns ranging in height from 10 to 25 cm. The following sequence of events was always observed. On starting the apparatus, sea water piled up in *F* until it reached a height (over the water level in *E*) equal to, or slightly greater than, the sand depth. It then blasted a narrow, rather tortuously ascending channel through the sand. As this happened, the pressure head in *F* fell to about half its previous height, where it remained, with a slight rise at each pulse. The ascending channel slowly widened and straightened as the water continued to flow up it, and acquired a very characteristic appearance. The flow rate was insufficient to blow the channel clear of sand. The channel was therefore full of eddying material which soon became roughly sorted and graded, with the heavier particles below and the lighter above. The system finally reached a steady state, with the perfusion pressure, in centimetres sea water, equal to about half the depth of the inflow hole below the mud surface.

The results of two typical experiments are reproduced.

In Fig. 7 *b*, the inflow hole (circle) was 10 cm. from the sediment surface. The stream blasted a tortuous channel (shaded), which slowly straightened and broadened. After 1 hr. it had acquired the outline drawn as a continuous line. Its contents were roughly graded, with coarse sand below, finer sand next, and a layer of floccules of light sediment (stippled) at the top; the whole was in continual pulsing, eddying motion. The system had settled down to run at a pressure which rose from 4·5 to 6·0 cm. at each pulse.

Fig. 7 *c* shows an experiment in which the inflow hole was 17 cm. below the mud surface. The first drawing (c_1) was made 1 hr. after the experiment started. There were wide columns of graded material above and below; in the middle (shaded), the channel was still narrow and tortuous, and blew clear of sand at each pulse; the percolation pressure at this stage was 5–6·5 cm. The second drawing (c_2) was made after a further 2 hr.; the channel had straightened itself considerably, and the system was running at 7–8·5 cm. pressure.

If, in these experiments, the flow was stopped for 10 min. or so after a steady state had been reached, the material in the channel settled and packed itself, with the heavier particles still below and the lighter above. On starting the apparatus again, the pressure head in *F* rose to a height a few centimetres above the steady-state level (though not as high as the initial blast level) before flow was resumed. The system rapidly returned to the previous steady-state pressure.

The density of the wet, muddy sand is roughly 2. The pressure head required for the initial blast is roughly equal to the depth of sand. These facts suggest that blasting consists essentially of the bodily raising of a column of sand extending from the inflow hole to the surface. When the column is lifted, it cracks and breaks up, and the lighter, muddy components are swept upwards. Thereafter, the lower part of the channel is filled with washed sand, which coheres less than the original mixture of sand and mud.

Remarks on the experiments. The following points emerge.

(i) To maintain an upward stream, in material of the kind used in these experiments, the worm must pump steadily at a pressure equal, in cm. H_2O, to half the height of the sand over its head. According to van Dam (1938), it can produce pressures of 10 cm. or more; according to Thamdrup (1935), it burrows to a depth of 20–28 cm.; evidently, then, it could irrigate an L-shaped burrow, once the initial blast had been achieved.

(ii) To produce this initial blast, twice the above pressure would be required. The maximum pressure that a pumping worm can produce is not known, and an enquiry into the point would be somewhat academic; the worm could reduce the necessary effort by tunnelling upwards, and there is plenty of evidence from field observations that it sometimes does so.

(iii) The upflowing water might well oxidize the iron sulphide in the mud and thus produce a yellow colour. Therefore, a yellow column, rising from the end of a lugworm's burrow, does not necessarily consist of surface sand.

(iv) The shaft produced by the water current would be vertical (except that it could curve round large stones and shells) and, to judge by the above experiments, some 1·5–2 cm. in diameter. As the head shafts found by the writer in the field were often much slenderer than this, and might be gently curved in the absence of obvious obstacles, it follows that other factors must play a part in their establishment and formation.

(v) The upward current would have an undesirable incidental effect, for its tendency would be to sweep the lighter particles upwards, leaving washed sand by the worm's mouth, and the lighter particles include the nutritious ones. This suggests that a conflict might arise between the means of oxygen supply and food supply.

In glass tubes, lugworms sometimes pump water in the reverse direction, from head to tail, and one might think that the conflict could be resolved if such reverse irrigation were the normal method under natural conditions. The following evidence, however, tends to exclude this possibility: (i) After many observations on worms in glass tubes, van Dam (1938) concluded that the current 'practically always goes from tail to head' in undisturbed worms, and that reverse flow appears to be a result of recent disturbance; Just (1924), who also watched worms in glass tubes, saw only the forwardly running waves; (ii) in the experiments with worms in sand-filled tanks, described below, I often saw swift currents flowing upwards in the head shafts, but I never saw any evidence of irrigation in the opposite direction; (iii) reverse irrigation in the field would draw sand between the worm's body and the wall of its burrow, and, except for the head shaft, a lugworm's burrow is always beautifully clear and open.

Evidently, we have two antagonistic processes at work. There is the downward movement of muddy sand, produced by feeding at the base of the head shaft, and the upward movement of water, which tends to wash the more valuable components away. We have now to see how these two processes can be reconciled.

The 'Working Up' of the Sand by the Worm

In another context (Wells, 1937) I devised a glass 'observation tube' in which lugworms lived for days or weeks, and their activities could be watched. Since then, I have put worms in observation tubes from time to time, and have noticed movements which may be of great importance in the working of the head shaft.

The observation tube is U-shaped, and of internal diameter 7–8 mm. (Fig. 8). Near its upper end, a narrow cross-tube connects the two limbs, so that the worm can circulate the contained sea water. Aeration is by means of a narrow capillary inserted into one limb, which is also widened above to facilitate the initial introduction of the worm.

The 'drag' cycle. To understand this performance, we must first note a feature of the worm, to which attention has only recently been drawn (Wells, 1944 *a*). The chaetigerous annuli of the more anterior segments have a special musculature, by means of which they can be raised into sharp, backwardly-directed flanges. The movement is best shown by the first three chaetigerous annuli; it also appears, to a progressively diminishing extent, in the next three or four. It is abrupt and vigorous; at one moment an annulus is flat, in the usual configuration; at the next, its whole circumference is raised, and the annulus itself seems to be distended with body fluid. All of these annuli rise and fall simultaneously (Fig. 8, inset).

In July 1942 I was watching a worm in an observation tube. It lay quietly at first, with its head at the bottom of the U and its tail up one limb. Suddenly it became restless, and crept forwards until its head was well up the other limb, and most of its body consequently vertical. It then repeatedly performed the following cycle of operations: (i) it gave three or four powerful extrusions of the proboscis, moving upwards a little as it did so, and lengthening and stretching the front part of its body exceedingly, as if to get its head as far up the tube as possible; (ii) it elevated its chaetigerous annuli, and slowly and steadily shortened itself, pulling its head down again; (iii) the annuli dropped back into the usual, flat configuration, and it began to work its head upwards again, so returning to stage (i). The whole cycle was carried out some half-dozen times.

Now, what was the worm trying to do? My first impression was that it wanted to grip the wall of the tube with the raised chaetigerous annuli, and so pull itself up. This interpretation was soon abandoned, for the same worm could creep up or down the tube in the usual way, forwards or backwards, with ease. Moreover, the hinder segments gripped the tube, and so acted as a fixed point, during the downward drag of the head. Clearly, the cycle could be used for a quite different purpose—to pull something down into a burrow.

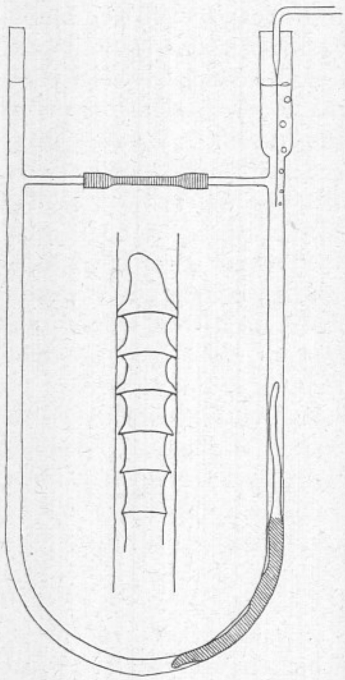

Fig. 8. Observation tube for studying the movements of *Arenicola marina*. Inset: the elevation of the anterior chaetigerous annuli.

I have seen the same action on several subsequent occasions. Sometimes the head is stretched out, beyond the end of the tube, into the air; then the annuli are raised and it is slowly pulled back.

The cycle could evidently be used to scrape and drag surface sand into an open funnel. As already noted (p. 172), several observers have described the worm's head as appearing actually at the funnel. From their accounts, this seems to occur only, or chiefly, when the burrow is submerged and the surface sand therefore soft. The worm might ascend, as Wesenberg-Lund (1905) and Blegvad (1914) suggested, to eat from the sides of the funnel; alternatively, it might collect surface sand by means of the drag cycle and pull it down into the shaft for subsequent consumption at leisure. As the proboscis is used in stage (i) of the drag cycle, the two possibilities would be hard to distinguish from each other in the field. In a predatory world, the second course would perhaps be the wiser one.

But the drag cycle could also be used in another way—to mix deeper material, softened by the ascending irrigation current, and so to combat the tendency of the current to sweep the lighter and more nutritious particles upwards. The broader of the head shafts found in the field (e.g. Fig. 2 *c*, *d*) can be supposed to be 'worked up' by the softening action of the water current coupled with mixing and stirring by the drag cycle.

Moreover, if the sand contains pebbles or large shell fragments, a rough sorting could be carried out by means of the drag cycle. The worm's head, as it drives upwards, would tend to push such objects sideways, and so to deposit them as a sheath around the central column of worked sand. Indications that this occurs were found while studying the burrows in wet, shelly sand (Fig. 4).

'*Piston*' *action.* I have sometimes watched worms in plain U-tubes, lacking the cross-tube shown in Fig. 8. Under these conditions, I have often noticed that the worm, while creeping forwards or backwards along a tube, may also occlude it; as the worm travels, one meniscus rises and the other falls; differences of pressure of 10 cm. or more can thus be set up.

This gives us an approach to the narrower of the head shafts found in the field. Such shafts are found both in rapidly drying and in wet sand. They consist of a tunnel or a sand column, of about the same diameter as the worm, rising to spread into a conical region below the funnel or saucer on the surface. The facts can be accounted for by supposing that the worm ascends to a point a few centimetres below the surface, then softens and mixes a cone of sand by means of the irrigation current and the drag cycle, then retires and pulls the semi-fluid sand into the passage along which it ascended, by means of piston action.

Indeed, all of the field appearances can be explained as resulting from the interaction of three factors—the softening of the sand by the irrigation current, the mixing and manipulation of the sand by the processes just described, and the subsidence of the worked-up material in consequence of feeding at the lower end of the shaft. The rejection of unsuitable materials will occur, partly (as just pointed out) during the drag cycle, and partly at the lower end of the shaft during feeding. It is in the latter situation that the smaller and the more flexible of the unwanted objects, which would not be thrust aside during the drag cycle, generally accumulate.

Burrows made in the Laboratory

In the hope of seeing these various factors at work, I kept a number of worms separately, each in a glass tank of wet sand. Fairly large worms were chosen (overall length 10–14 cm.) and the volume of sand was small; by this means, the worms were induced to set up head shafts against the glass, where they could be observed in detail.

The tanks had a horizontal sectional area of 11×17 cm. and were filled with muddy sand to a depth varying in different cases from 14 to 19 cm. The sand was stratified, to make the conditions as normal as possible; most of it was grey-black material, dug fairly deeply from the beach, but a layer of yellow surface sand was put on top. Finally, the whole was covered with a couple of centimetres of sea water, so that the worms could irrigate their burrows.

Beyond aerating the sea water, and occasionally adding distilled water to compensate for evaporation, no further precautions were taken. The worms lived actively in the tanks for many weeks. My records cover (i) four worms, kept under observation for 30 days, and (ii) confirmatory experiments on five others, kept for various periods (up to 3 months) and observed from time to time.

The worms themselves were seldom seen. Their behaviour was inferred (i) from the position and amount of their faeces, which were cleared away whenever they were noted, to facilitate further observation, and (ii) from the forms and changes of the head shafts.

The faeces. In most cases there was a preliminary period of 'settling down', lasting for 24–48 hr., when a worm was first put in a tank. During this time, no faeces appeared.

After this period, the worms, with one exception, defaecated at least once a day, and generally much more often. The single exception defaecated little and seldom, and sometimes missed out a day altogether. This peculiarity was kept up throughout the month of observation. There seemed to be considerable individual differences in this matter; other worms consistently distinguished themselves as abundant defaecators.

At the same time, the frequency of defaecation often fluctuated in any one worm. A vigorously active individual would regularly produce a cylinder every 25–45 min., for many hours, and this could be kept up day after day. Sometimes, however, a worm defaecated every half hour or so on one day, but rested for three or four hours at a stretch on the next.

The position at which the faeces appeared was very constant. Of the four worms studied for a month, the first always defaecated at the same point; the second changed its position once by reversing the burrow, the faeces thereafter appearing at the top of the old head shaft; the third made two changes, reversing its burrow on one day and returning to the old orientation 3 days later; the fourth changed three times, once by reversal and twice, on consecutive days, by breaking new ground.

Few of the investigators of the form of the burrow have concerned themselves with its permanence. The most direct observations on this point are by Schwarz (1932) and by Thamdrup (1935). The former pointed out that the funnels and faecal piles may become very large in situations sheltered from wave action, suggesting that the worm lives in the same burrow for a considerable time. According to the latter, the permanence of the burrow depends to some extent on its situation; if the sand is not much disturbed by wave action, the burrow is inhabited at least for weeks on end; this conclusion rests on observations of worms in a large aquarium, on the watching of marked burrows on the beach, and on the dimensions of funnels and faecal piles in sheltered situations; the burrows are probably changed more frequently in places where the surface is often disturbed. My own aquarium observations confirm this general conclusion, as regards the faecal ends of the burrows; we shall see later that the head shafts were changed rather more often.

Head shafts seen in section. Head shafts were made, sometimes against the glass and sometimes away from it. In the former case they were seen as it were in section.

I never saw an open, ascending passage, ending above in a funnel, as required by the 'open U' form of burrow. The head shafts were broad, typically vertical columns of 'worked' sand, often very like those produced by the artificial irrigation currents described above. Ascending streams of water were frequently seen in the shafts.

A typical example is shown in Fig. 9 *a*, with the outline of the worm included to scale below. This shaft was set up in the corner of the tank, so the page should be imagined as folded backwards at right angles along the vertical line.

The first observed signs of this shaft were a conical depression of the surface, and an irregular cavity, with a domed roof, about 9 cm. below it. This stage is shown by thick outlines in the figure, the cavity being shaded.

On the following day the shaft had assumed its definitive form. It was now very like an artificial irrigation channel, and consisted of loosely packed sand, with a layer of light sediment, 3 cm. deep, at the top. It differed from the artificial channels in that a funnel had developed at its upper end, due to the animal's feeding from the substance of the shaft. This stage is drawn as a thin outline, the horizontal line being the top surface of the sediment.

The worm continued to work this shaft for a fortnight, at the end of which time it had acquired the outline shown as a dotted line in the figure. The processes actually seen during this period were (i) crumbling away of sand from the sides of the funnel, (ii) upward streaming of the irrigation current, now on one side of the shaft and now on the other, (iii) slight erosion of the side walls of the shaft by the stream, causing gradual broadening of the column, and (iv) on one occasion, pulsing movements of the sand suggesting that the drag cycle was being carried out somewhere within it. The worm itself was never seen. At the end of the fortnight, the whole column had acquired a striking yellow colour, like that of the surface layer of the sand, into which it appeared to continue. This coloration was doubtless due, in part at least, to oxidation by the irrigation current.

Several shafts, resembling this one in general pattern, were set up during these experiments. The first signs of their formation were (i) slight subsidence of the surface, accompanied by (ii) the appearance of irregular cavities, often with vigorous upward currents in them, further down. Sometimes black silt, obviously swept up from below, appeared on top of the yellow surface layer of the sand. From the first, then, it seems that feeding and irrigation were at work together.

The shafts soon settled down into broad, rather loosely packed columns, with light sediment above, and with funnels round their upper ends. The sand grains in the columns did not grade themselves as perfectly as did those in the artificial irrigation channels; except for the top layer of sediment, the

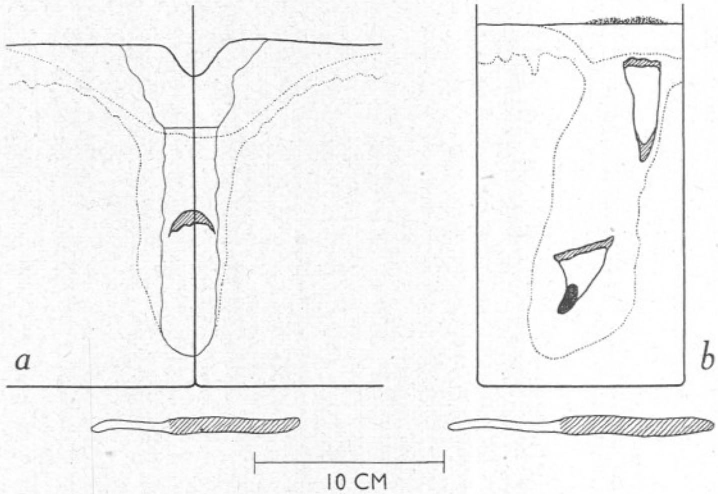

Fig. 9. Stages in the development of head shafts in glass tanks. The worm responsible for each shaft is drawn to scale below it.

substance of a column was pretty homogeneous. This probably resulted from two factors. First, the worm drove the upward stream, now on one side of the column and now on the other, and this seemed to have a stirring effect. Secondly, on several occasions, pulsing movements of the sand were noticed, suggestive of the drag cycle. To my sorrow, however, the worms were never actually seen to carry out the cycle. On the rare occasions when parts of the worms were visible, they were working at the lower ends of the shafts.

Irrigation was always intermittent. When a worm began to drive water upwards, the level of the top of the column rose several millimetres, due, presumably, to the forcing of water in among the sand grains with consequent increase in volume of the column. It sank again when irrigation ceased. Bohn (1903) saw very similar oscillations of level in funnels on a sand bank, as the tide was just flowing off it.

On probing the head shafts, their texture was found to be exceedingly soft, as one might expect; in this respect, they resembled the upper parts of the head shafts found in wet sand in the field.

An interesting, if rather atypical, shaft is shown in Fig. 9 *b*. The first observed stage is drawn with thick outlines, the cavities being shaded. Below, there was a triangular area of 'worked' sand with a cavity at its upper side and a glimpse of the worm's head (black) at its apex. Nearer the surface was a second triangular area with clefts at both ends. Vigorous upward currents were seen in the substance of both areas. Finally, there was a thin layer of upblown black sediment (stippled) on the surface. These various signs clearly indicate an irregular, somewhat oblique shaft, partly against and partly away from the glass. Its obliquity is interesting, and suggests that the worm had tunnelled upwards nearly to the surface as a preliminary stage in its establishment. The setting up of a shaft appears, then, to involve all of the three factors, feeding, irrigation and upward excursion.

This shaft was worked for three weeks, during which period upward currents and occasional clefts appeared in various places. The final result was a wide area of yellowish, 'worked' sand, still rather oblique, whose boundary is drawn as a dotted line in the figure. This shaft was made by the worm which defaecated little and seldom, hence the comparatively slight depression at the surface.

Head shafts seen from above. When head shafts were set up away from the glass, they presented the appearance, as seen from above, of gradually enlarging and deepening saucers, often with a flat bottom of fine sedimentary material, and closely resembling those seen so often on the beach.

The irrigation current escaped either diffusely (in which case the water in the saucer was often hazy or cloudy in appearance) or through 'blow holes', i.e. circular areas, a few millimetres across, walled by low parapets of upblown material, and containing sediment in intermittent, eddying motion. A blow hole would appear at some point in a saucer, to disappear after several hours and perhaps be replaced by another elsewhere. Similar blow holes are often seen in the saucers in wet sand on the beach.

The first stages in the formation of a saucer were very variable. An area, a couple of centimetres across, might be outlined by two or three fine cracks, and then gradually subside to form the bottom of a saucer; or a ragged hole, 1 or 2 cm. across, with steep walls and a cloudy, turbid interior, might be the first sign, the saucer later developing by inward crumbling of its margin. Once again, these observations are paralleled by others made on the beach (p. 184).

General remarks on the head shafts. The head shafts were changed rather more frequently than the defaecation points. For example, after the worm had worked the head shaft of Fig. 9 *a* for 2 weeks, it became restless and, in the next 5 days, it set up three new head shafts, at the sides of the old funnel. It continued, however, to defaecate from the old point. The phenomenon of changing the head shaft while retaining the old defaecation point was often noted during these experiments. It has also been observed in the field, both by Thamdrup (1935) and by myself (Fig. 2 *h*).

Occasionally, a worm defaecated copiously for a day or so, during which no sign of a head shaft could be seen, either against or away from the glass. The longest period for which such behaviour continued was 4 days. I have no explanation to offer for this observation.

It was suggested, in a previous section, that the main factors in the working of a head shaft are feeding and subsidence, the irrigation current, and upward 'working' excursions of the worm. In the experiments now described, whose main purpose was to test that statement, the importance of the first two was clearly demonstrated—of feeding and subsidence by the gradual development of the funnels at the upper ends of the shafts, and of the irrigation currents (which were frequently seen) by the general structure of the shafts and their top layer of light sediment. The existence of upward excursions was inferred, on rather less solid grounds, from the obliquity of the shaft in Fig. 9 *b*, from occasional pulsing movements of the sand suggestive of the drag cycle, and from the imperfect grading of the sand in the shafts.

In comparing the results with those of the field observations, it must be borne in mind that the tidal factor was lacking in my experiments. There was no supply of fresh material at the upper ends of the shafts (except for insignificant depositions of faecal matter when the faeces were periodically destroyed) and the worms were able at all times to irrigate their burrows. The latter consideration may be important; the behaviour of the worms, and the consequent structure of the head shafts, may be greatly affected by the periodic 'cutting out' of irrigation at low tide, with its inevitable effects on the mechanical properties of the sand.

The experimental results may be regarded as a model of the worm's normal high-tide behaviour, while the field observations were naturally made at low tide. The worm's life is an alternation of the two modes. We may suppose that the submerged worm works up and softens the sand by the processes already described. In the case of the wider shafts, the whole, or a large part, of the shaft may be so treated. In the case of the narrower ones, the working may be confined to the upper, conical portion and followed by the drawing downwards of a narrow column of softened sand. At low tide, feeding and a certain amount of working up may continue if the sand is soft and wet, but these activities will presumably be greatly slowed or altogether stopped if the sand dries and hardens. With the return of the tide, irrigation can be resumed, and the head shafts can be extensively reconstructed if necessary.

Notes on Food Supply and Oxygen Supply

The following notes arise from observations made incidentally during the course of the work.

The Food of the Lugworm

Lugworm faeces are generally yellow, like the surface sand, but black or grey-black faeces sometimes occur. While working in the field, both at Bangor and at Aber, I always noticed a sprinkling of dark castings among the much commoner yellow ones. The worms kept in tanks, as described in the last section, usually produced yellow faeces, but sometimes black or grey faeces appeared.

The colour of the faeces presumably depends on that of the sand on which the worm happens to be feeding. It would be difficult to explain the following laboratory observation in any other way. A worm, which was setting up a new head shaft, produced a cylinder consisting of 4 cm. of yellow matter followed by 3 cm. of black, the two separated by a sharp boundary though both forming parts of the same faex. Twenty minutes later, it shot out an even more remarkable one—2 cm. black, then 1 cm. yellow, then 2 cm. black, and finally 2 cm. yellow—again with sharp boundaries. The subsequent faeces were all yellow. The worm must have fed alternately from black and yellow sand, and refrained from mixing its successive ingestions as they passed down its gut.

The occasional black faeces seen in the field indicate, then, that the worms sometimes consume the deeper sand. In the laboratory experiments, the appearance of black faeces generally coincided with a change in the configuration of the burrow, such as the establishment of a new head shaft. During the early stages of formation of a head shaft (e.g. those shown by thick outlines in Fig. 9), the deep material is still black, and its consumption is demonstrated by surface subsidence and the appearance of cavities deep in the sand. Worms feeding from well-established head shafts nearly always produced yellow faeces. Exceptions, however, occurred; thus, one worm produced copious masses of grey-black faeces every day for a fortnight, for most of which time it was apparently working a single head shaft, set up away from the glass, but plainly visible as a gradually deepening, saucer-shaped depression of the surface.

A yellow casting—and the ones in the field are mostly yellow—shows that the worm has eaten yellow sand. It also suggests that the worm has eaten surface sand, but this inference is less secure than the first, since the ascending irrigation current might turn the deeper sand yellow. In fact, however, a well-established head shaft seems to be, in the main, a descending column of surface sand; downward motion is shown by the shelly and vegetable fragments which frequently collect at the lower end, and by the subsidence of the funnel; renewal from the surface and by sedimentation must take place if the shaft is to be maintained. A certain amount of deeper material may get mixed in with it, partly owing to the activities of the ascending and descending worm, and partly owing to the eroding action of the irrigation current on the walls of the column; the shafts seen in the laboratory tanks slowly widened, and a similar widening probably occurs in the field.

The frequent collections of fine shell fragments, pieces of weed, dead leaves and so forth at the bottoms of the head shafts are evidence that selection occurs at the moment of feeding, even if it is limited to the rejection of mechanically unsuitable objects. Sometimes, however, quite large pieces of animal or plant material are swallowed. Ashworth (1912) states that pieces of seaweed are occasionally found in the alimentary tract of *A. marina*, and Saint-Joseph (1894) remarks: 'dans le corps d'un exemplaire j'ai trouvé une Néréide entière presque digérée.' Whether these soft objects were accidentally engulfed with the sand, or whether they were deliberately selected, is not known. One would have to examine the contents of a large number of specimens, preferably from different situations and at different seasons of the year, before deciding whether such ingestions occur with dietetically significant frequency.

Oxygen supply: aerial respiration

Lugworms can absorb oxygen either from water or from air. The latter point is emphasized by van Dam (1938): 'in my tests *Arenicola* was seen to live for several days in damp air of room temperature.'

At high tide, both ends of the burrow are submerged. We have seen that the worm can irrigate the burrow under these conditions, so securing an adequate oxygen supply, even if the burrow is not an open U.

At low tide, the conditions vary with the situation. I found, on rapidly drying sand patches, that the water drained away to such a depth that the burrows were completely air-filled. There will be no great difficulty in this case, provided the air is damp. More often, on the other hand, the burrow is wholly or partly filled with water, which the worm is unable to circulate. This water will lose its oxygen, partly to the worm and partly, perhaps, to the surrounding sand, and the worm may therefore find itself exposed to oxygen lack. What will it do?

Lindroth (1938) showed that *Nereis* (*diversicolor* and *virens*), in a U-tube of water deficient in oxygen, draws air bubbles between its body and the tube and holds them there. Van Dam (1938) discussed the possibility of spontaneous aerial respiration in *Arenicola*, but was unable to demonstrate it: 'if, however, animals were put into a glass U-tube partly filled with water, they did not creep into the air of the tube even after a number of hours; at most they protruded their head or tail about 1 cm. above the water.'

I was more fortunate. On putting worms into U-tubes partly filled with sea water, which they were unable to circulate, I repeatedly saw what appears to be a method of aerial respiration. After an hour or so, they crept backwards to the surface of the water, with their tails curled up into a pretty tight screw (as if to make them as short as possible); they then drew air down between their dorsal surfaces and the tube, and held it there. The 'trapped' bubble usually covered several pairs of gills. This behaviour was not invariably obtained. The most successful experiments were done within 24 hr. of the collection of the worms, and in a light so dim that one could only just see what the worms were doing. Probably a bright light has an inhibiting effect on the behaviour of *A. marina*.

Clearly, 'bubble-trapping' could be very useful in wet sand at low tide. It could conceivably alternate with other activities, the haemoglobin being used for oxygen storage. Thus, the worm might oxygenate its haemoglobin after each defaecatory excursion, then go down again to resume feeding.

In the above remarks, it was assumed that the worm is in a well-established burrow. Special conditions will arise while a burrow is being constructed or altered. On putting the worms into the experimental tanks described above, they vanished into the sand, and 24–48 hr. often elapsed before any faeces, or any sign of a head shaft, were seen. It would be interesting to know how they secured an oxygen supply during that time.

Summary

The Form of the Burrow

1. The burrows were studied in various situations (rapidly drying sand, wet sand, shelly sand, gravelly and stony places), all in the neighbourhood of Bangor, North Wales.

2. The burrow typically consists of a gallery, a tail shaft and a head shaft (Fig. 10, 204).

The gallery is a roughly L-shaped tunnel, whose walls are impregnated by the worm's secretions and marked by its neuropodia. The worm moves to and fro in the gallery, with its tail towards the upper end.

The tail shaft is a short portion connecting the upper end of the gallery with the exterior, and housing the worm's tail at the moment of defaecation. It may have two or more orifices, and it lacks neuropodial markings.

The head shaft connects the lower end of the gallery with the surface, and is exceedingly variable in structure. The most typical form occurs in wet sand. In this case the head shaft is a column of yellowish sand, one to three times as wide as the gallery, rising towards the surface and there spreading into a cone below a saucer-shaped depression. In other situations many variations are encountered; the shaft may, for example, be a broadly spreading cone of sand; it may include an open passage, of the same diameter as the gallery; it may be complicated by the presence of shell fragments or other objects.

3. In the second of these variations, the burrow is an open U. Such burrows were found only in rapidly drying sand, and appear therefore to be exceptional. Moreover, the ascending passage in an open head shaft lacks

the mucus-impregnated wall and neuropodial markings of the gallery, and seems to be of less permanent nature.

4. Evidence that the worm feeds at the lower end of the head shaft is given by the frequent accumulations of weeds, dead leaves and so forth at the bottom of the shaft. These objects are left in the surface saucer by the receding tide, travel down the shaft, and are rejected by the feeding worm below.

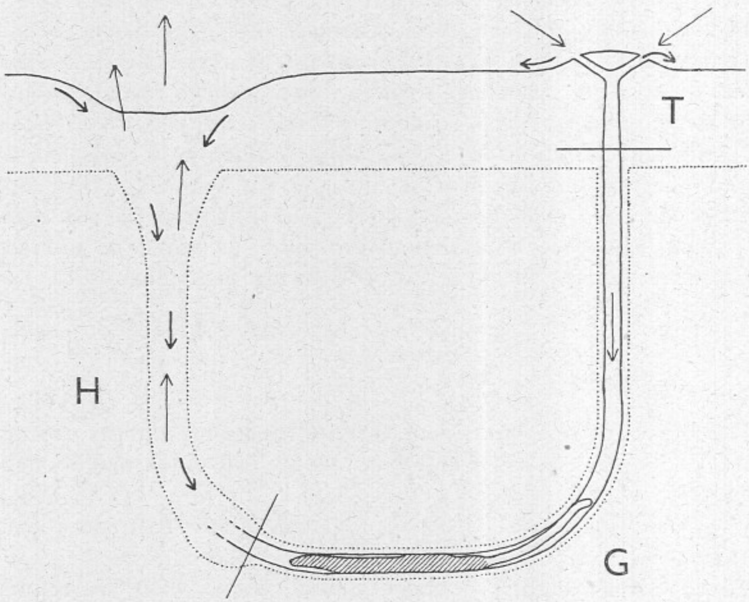

Fig. 10. Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

According to Thamdrup (1935), the head shaft is a column of down-sliding sand which originates and is maintained by the worm's feeding at the lower end. Doubt is thrown on this suggested mode of origin by two facts: (i) the head shafts, even in wet, shell-free sand, are often slightly curved, and (ii) worms can live in shelly and gravelly situations where the setting up of a shaft along these lines would be quite impossible.

5. Many signs show that the worm ascends the head shaft from time to time. Obvious ascending tunnels, of the same bore as the gallery, were frequently found in rapidly drying sand. That the typical, wet-sand head shafts are shaped in the first place by upward excursions of the worm is suggested (i) by the fact that the narrowest head shafts have about the same

diameter as the gallery, and (ii) by a single case in which a wet-sand shaft contained an impress of the worm's body near its upper end.

6. The head shafts encountered in shelly and gravelly situations cannot have arisen by deep feeding and subsidence alone; they must have been produced by complicated 'working' activities of the worms.

The Working of the Head Shaft

7. A laboratory study has been made of the processes by which *Arenicola* works its head shaft.

8. The worms drive water through their burrows by means of special waves travelling forwards along the body. Water currents were liberated into muddy sand and their course and effects on the sand were noted. The results show that a lugworm could irrigate an L-shaped burrow; the water would rise from the blind end of the L and form a vertical shaft, about 1·5–2·0 cm. across; the shaft would consist of graded material, with coarse sand below and fine sediment above, and it might be yellowed by the ascending stream.

Such water currents might be important in softening the sand in the head shaft, but the shapes of head shafts found in the field show that they cannot have been formed by the irrigation current alone.

9. While watching worms in glass tubes, two types of movement were seen, which are probably of great importance in the working of the head shaft. They are (i) the 'drag' cycle, in which the head is thrust upwards, then the anterior chaetigerous annuli are raised into flanges and the head is pulled slowly back again, and (ii) 'piston' action, in which the worm creeps along a tube, at the same time occluding it, and so drawing water through the tube.

10. The various head shafts seen in the field can be explained as arising from the interaction of three factors: (i) the softening of the sand by the irrigation current, (ii) upward excursions of the worm, with special activities like those just described, and (iii) feeding from the base of the head shaft.

11. A number of worms were kept individually for many weeks, each in a glass tank of muddy sand under sea water. When head shafts were set up away from the glass, their appearance resembled in every way those seen on the beach. When head shafts were set up against the glass, they were seen to be columns of sand, continually perfused by the ascending irrigation current; they gradually broadened and yellowed; conical depressions developed at their upper ends, due to the feeding of the worms from their substance; occasional pulsing movements of the sand suggested that the worms were carrying out the drag cycle somewhere inside the shafts.

12. In the tank experiments, the defaecation points were seldom changed; the positions of the head shafts were changed rather more often. These results confirm the conclusion of Thamdrup (1935), that a lugworm inhabits a single burrow at least for weeks at a stretch, if the conditions are favourable.

Notes on Food Supply and Oxygen Supply

13. The occasional occurrence of black faeces, both in the laboratory and in the field, shows that *Arenicola* sometimes consumes the deeper sand, although its chief diet seems to be the downwardly moving surface sand in the head shaft.

14. In a U-tube of stagnant water, *Arenicola* often rises backwards to the water surface and draws air bubbles down into contact with its gills, thus proceeding spontaneously to aerial respiration. This behaviour could be useful at low tide, when the burrows are often filled, or partly filled, with stagnant water.

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